Information on Bird Navigation Obtained by British Long-Range Radars

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In the years 1958 to 1963 several British ornithologists were permitted to make observations of bird migration with surveillance radars of the Royal Air Force. These radars were superseded by more modern equipment in the early 1960's and access was then terminated. Thus the data used in this review refer to a period of observation nearly 10 years ago, though the analysis and interpretations are recent.

The radar equipment was a 10-cm surveillance antenna of the type described by Eastwood and Rider (ref. 1). It was of high power, such that a single "echo" from birds often could be tracked for 150 km and sometimes for over 200 km. Echoes were displayed on a plan position indicator (PPI) and records were made either directly from the display or by time-lapse photography (ref. 2). No moving target indicator facility was available. My own observations were made at a site in Northumberland, northeast England, in the autumns of 1961, 1962, and 1963 and in the spring of 1963.

Certain limitations of long-range radars are recognized in assessing the observations of birds in flight. The major disadvantage is large pulse volume. All reflecting objects within the pulse volume contribute to a single echo on the radar display. At about 60 km from the antenna, the pulse volume is the product of an area of resolution of about 0.67 km^2 with an altitude range from the ground to an altitude above the normal level of bird flight. Thus, a single echo on the radar display can correspond to any number of birds, depending on density and flocking behavior of migrants. At longer ranges, resolution of the radar deteriorates. Nisbet (ref. 3) has used this relationship to extrapolate simultaneous counts of echo densities at different ranges to derive a value at zero range, where resolution is greatest. By comparing this density with the migration density derived from counts of birds passing a siting of the Moon on the same night, he was able to calculate an average number of birds per radar echo and quantify the radar observations. Similar quantification was not possible where I was in northern England because of cloudy skies. Thus observations reported in this paper refer to numbers and directions of movement of echoes and not of single birds.

Findings relevant to the problems of bird

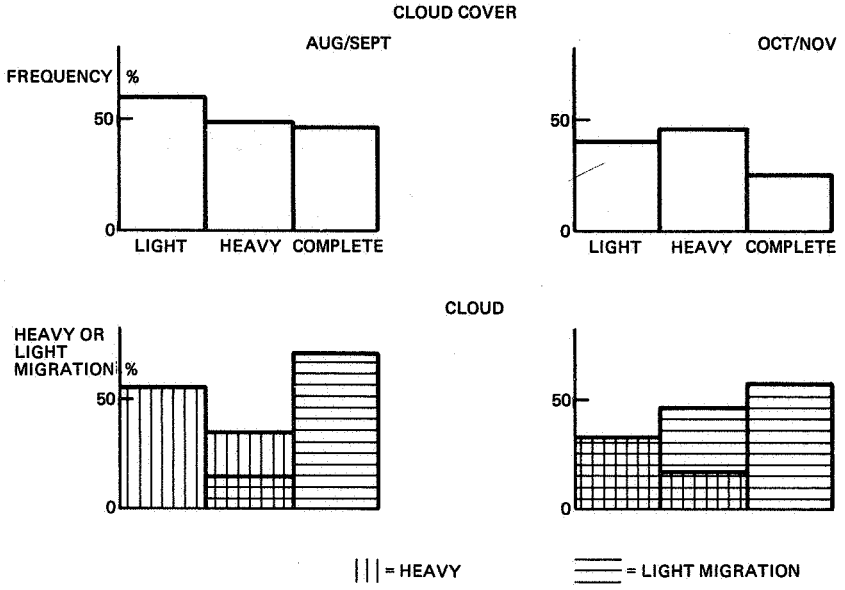

FIGURE 1. Relation between intensity of cloud cover and frequency and density of SSE migrations of passerines in northeast England, 1961 to 1963. Frequency of migration is given as percentage of nights with the particular weather condition on which migration actually occurred. Densities of migration are given as the percentage of nights of actual migration when heavy or light movements, respectively, were recorded. (Heavy + medium + light migrations = 100 percent).

navigation were: migration under total overcast; compensation for wind drift; reorientation after displacement; reversed movements; and changes in direction of flight during migration. These findings will be discussed using observations of passerine movements to the SSE in the fall and to the NNW in the spring.

MIGRATION UNDER TOTAL OVERCAST

Complete cloud cover was recorded over the area covered by the Northumberland radar on 42 of the 193 nights of observation in the autumns of 1961 to 1963. On 12 of these nights, rain echoes obscured the radar display of any bird echoes there might have been. Migratory departures were seen on 17 of the remaining 30 overcast nights. Thus birds were not deterred from setting out on migration under total overcast, although fewer did so on such nights than on clear nights (fig. 1). As soon as birds could be detected by radar they were correctly oriented, though it is not known whether they were flying above, in, or below the cloud layer. On several nights the birds departed under total overcast, with fog at ground level; landmark orientation would have been impossible on these nights. Further details are documented by Evans (ref. 4).

A similar picture is given by radar observations of passerines in the spring of 1963. Of 22 nights of total overcast, rain echoes filled the display on four nights. Migration was seen on 12 of the remaining 18 nights. Two departures were observed through fog at ground level. Departures of migrants under

complete cloud cover have been recorded for shorebirds as well as for passerines (ref. 5). These observations suggest that orientation by the stars is not the only method available to night migrants.

COMPENSATION FOR WIND DRIFT

From analyses of night-to-night variation in the mean direction of autumn migration, I concluded that both passerines and waders compensate in flight for wind displacement and fly on preferred tracks rather than on standard headings (refs. 4 and 5). This conclusion was based on four lines of argument:

(1) The night-to-night variation in track direction was less than in headings. This was true both in August and September when the chief migrants were warblers and chats, and in October and November when the chief migrants were thrushes.

(2) The mean track direction on nights when the winds blew from the right of the tracks was almost identical with the mean track when the winds blew from the left of the tracks. This finding held for the two groups of passerine migrants and for movements of shorebirds.

(3) The heaviest migrations did not take place with directly following winds, when track and heading would have coincided. On the five nights of heaviest migration in August and September of 1961 to 1963, wind drift was such that birds were blown between 25 and 80 miles away from their headings for every 100 miles they flew. Thus it seems unlikely that birds were trying to maintain preferred headings.

(4) The mean direction of migration did not change during the night, even when the direction of the upper-air winds changed by as much as 110°. This was true on five nights in September and another five in October and November, so that the finding applied to both groups of passerines. (Details are given in ref. 4, tables 6 and 10.)

The conclusion—that birds compensate for wind drift—is in agreement with the findings of Nisbet and Drury (refs. 6 and 7) and Bellrose (ref. 8) in America, but contrary to Lack's (ref. 9) original interpretation of his radar observations in eastern England. Lack's observations were interpreted again, independently, by Evans (ref. 4) and Nisbet and Drury (ref. 7). They based their interpretations on a model that required birds to compensate for drift in flight; but the model predicted that a larger proportion of migrants whose intended tracks were wind-assisted would depart on a given night, as compared to the proportion of birds whose tracks were partly opposed by the wind. Further details of this "selective departures" hypothesis are given in references 4 and 7. Lack (ref. 10) has reanalysed his data, and now agrees that birds keep to chosen tracks under most wind conditions.

The implications of this conclusion need to be considered. Perdeck (ref. 11) has suggested that young starlings (*Sturnus vulgaris*) reach their winter quarters on their first migration by a "direction and distance" process. The ability to keep to a chosen track direction in flight, as demonstrated above, would seem an essential attribute. But so also is an ability to measure distance. How might this be done?

The simplest method would appear to be flight for a predetermined time, but the distance traveled in a fixed time could vary widely with wind conditions unless a bird could hold its groundspeed constant. This implies that it would vary its airspeed. Yet Pennycuick (ref. 12) has shown on theoretical grounds that there is a certain airspeed that should be maintained by a bird of a given species and known weight if that bird is to achieve maximum flight range in still air. (A

bird's weight decreases as its fat reserves are used up during migration, and its cruising speed must also decrease to maintain maximum range speed.) If a bird adopts this strategy, then its groundspeed will be the vector sum of cruising speed and wind. Hence flying for a fixed time will not enable birds to fly a chosen distance.

In practice, however, recent radar studies by Schnell (ref. 13), Bellrose (ref. 8), and Bruderer and Steidinger (this volume) show that birds of several species seem to maintain more nearly constant groundspeeds than would be expected under a variety of wind conditions. Schnell's data, however, do not refer to birds on migration. Therefore, his findings are not unexpected, since Pennycuick's calculations show that the cruising speed for sustained migratory flight is only one of a range of airspeeds of which they are capable for flights of much shorter duration.

Bellrose's observations warrant further discussion. He found that the groundspeeds of migrants were not influenced in proportion to the favorable component of the wind force, and concluded that migrants reduced their own efforts as windspeed increased. He noted this phenomenon even on single nights, when the effects of different windspeeds presumably were examined by choosing birds flying at different altitudes and in different directions. His method of analysis—plotting the regression of groundspeeds of migrants against appropriate wind forces—is valid only if the same bird species may be found flying at any chosen altitude or under any wind conditions. I suspect that this condition does not hold. An alternative way of expressing Bellrose's conclusion is that at high (following) wind forces, the mean airspeed of the migrants recorded in flight is lower than that of birds flying at low wind forces. This might come about as follows: Birds probably choose the altitude and wind conditions in which to fly—so that migrants with the lowest cruising airspeeds might fly only with a large favorable component of wind force, whereas migrants with higher airspeeds are prepared to fly with less favorable winds. In a single migratory flight this might lead to a stratification of airspeeds with altitude, so that birds with low cruising speeds flew higher (to gain larger favorable components of the wind) than those with higher cruising speeds. Such stratification could be reinforced by the need for birds with higher cruising speeds to remain at lower altitudes to maintain adequate oxygen intake.

Until such possible alternative explanations of Bellrose's observations have been discounted, I remain skeptical of the possibility that a migrant's groundspeed is maintained relatively constant in a variety of wind conditions. Hence, I am still doubtful that a chosen distance can be achieved by flight for a chosen time. In any case, if birds conform to Pennycuick's predictions and always fly at maximum-range airspeed, the distance traveled in one hour by any bird will depend on its initial weight, which will vary during the course of migration.

Distance flown might also be measured by the rate of loss of fat reserves, but this rate depends on the power requirements of the bird, which in turn are affected by the problem of constancy of airspeed discussed above. Hence, loss of fat is a poor index of distance traveled. If distances are to be measured reasonably accurately by a juvenile bird migrating to winter quarters, there seems no easy way other than by comparison of coordinates of the starting and finishing points. (The hypothesis could then be made that when the distance so calculated equals an internally programmed distance, migration in that direction should terminate. Alternatively it should terminate when the migrant reaches a point whose coordinates are inherited—in

which case no distances need to be calculated.)

To return from his speculation, a direct consequence of the method a bird uses to compensate for wind drift is that there are certain wind conditions when compensation becomes physically impossible. Normally a bird heads somewhat into the wind to maintain its chosen track. If the wind is opposed to this track and is stronger than the bird's normal cruising speed, then a bird trying to compensate will be blown backwards. I have suggested elsewhere (ref. 4) that even before the speed of an opposed wind reaches the cruising speed of the bird, a migrant may allow itself to be drifted from its preferred course. The consequences of drift from the normal migration route will now be examined in a "natural experiment" in Western Europe.

REORIENTED MOVEMENTS

In August and September of 1961 to 1963, there were no regular migrations of passerines from Scandinavia to northeast England, as seen by radar. Yet in these same months every year, SSW movements of passerines are often seen by radar some 320 km farther south, in East Anglia (refs. 14 and 15). I believe these to be the western fringe of direct migration from Scandinavia to Iberia, though I am aware that many migrants probably leave Scandinavia in a more easterly direction (see, e.g., refs. 4, 16, 17). Under certain weather conditions, particularly with strong SE (opposed) winds, this western fringe of migrants can no longer hold its SSW course, and birds have no option but to be blown westward. They then alight in considerable numbers on the coasts of northeast England and eastern Scotland. Among the most numerous species are redstarts (*Phoenicurus phoenicurus*), garden warblers (*Sylvia borin*), and pied flycatchers (*Ficedula hypoleuca*), all of which are typical Scandinavian species; most of the birds are juveniles.

The fate of these birds, blown off-course, is of considerable relevance to ideas of how young birds reach their correct winter quarters in the absence of parental guidance during migration. Perdeck (ref. 11) has shown that young starlings, when displaced artificially from their normal migration route, fly parallel to that route. If the wind-displaced Scandinavian migrants did the same, i.e., flew SSW from northern Britain, they would fly out over the Atlantic and be lost. It seems, however, that in practice they compensate for their westward displacement and reorient toward their correct migration route. They do this even though they fly singly (ref. 18) and without calling in flight at frequencies audible to human ears; it seems, therefore, to be within the capacity of individual juveniles to reorient. The evidence for reorientation is threefold:

(1) Recoveries of displaced birds caught and banded in northern Britain come from the same parts of France and Iberia as those of birds caught in southern England during pauses on their normal migration. Furthermore, the percentage of banded birds subsequently recovered is the same for displaced birds of a given species as for undisplaced birds. Full details are given by Evans (ref. 16).

(2) When tested in orientation cages in northeast England, all but one of the displaced migrants which showed clear orientation did so in a direction eastward of their presumed original direction of SSW. They had thus compensated for westward displacement. Some compensation would have arisen merely if their internal clock had remained in synchrony with the longitude from which they had been displaced. But since they

moved westward no more than 15° of longitude, the maximum shift of their preferred orientation would have been 15° eastward, i.e. from SSW to just west of south. In fact, all shifts recorded were greater than this (ref. 16).

(3) After a very heavy arrival of Scandinavian migrants in northern England on August 31 and September 1, 1963, all departures of these birds (on the nights of September 2 and 3) were seen by radar to be indistinguishable in direction from the SSE mean direction taken by departing British migrants (ref. 4). While there was a spread of directions about this mean of SSE, all tracks lay east of south, implying that birds had shifted their heading eastward, and by more than the 15° shift discussed above.

In summary, the directions of reorientation shown by these displaced migrants would have taken them back to their migratory routes before they reached the areas in Iberia where banded birds were recovered. It is not known where rest and feeding areas for Scandinavian migrants are located in southern Europe. (Perhaps there are no specific areas, but each migrant rests and eats where it can, prior to the trans-Saharan crossing.) Hence the significance of the departure directions detailed above cannot be interpreted at present in terms of headings toward definite staging areas on a migratory route.

As an alternative to reorientation toward an intermediate staging point, whose coordinates the bird must know, Matthews (ref. 19) suggested that a bird might derive a reoriented direction by vectoring its standard direction of migration (at the time and origin of displacement) with the direction joining the origin to the point of arrival after displacement. To obtain accurate reorientation, the bird would have to measure distances accurately, and I believe this can be done only by comparison of coordinates, as discussed earlier. We do not know, however, how accurate reorientation really is. Hence an evaluation of the two possible mechanisms of reorientation cannot be made at present.

REVERSED MIGRATIONS

On several autumn nights, the migration seen by radar was in a direction exactly opposite to that expected, i.e., birds flew NNW instead of SSE, and no movement could be detected in the normal direction.

An analysis of weather data for the 17 reversed movements seen in the autumns of 1961 and 1962 revealed the following relationships:

(1) The surface winds on all nights were less than 10 knots, and from between SE and SW. They were thus opposed winds for normal migration. Yet normal SSE movements occurred on 52 percent of nights with light opposed winds in August and September, and 36 percent in October and November during the study period (fig. 2).

(2) Temperatures at 1800 hours, close to the time of departure, were very close to the long-term norm for the days of observation. (On only one night was the temperature more than 1°C above normal.)

(3) Cloud cover was complete on only three of the 17 nights; on another six nights, cloud cover was less than half.

(4) On five occasions, reversed movements occurred on two nights in succession.

In summary, these movements were not disoriented, nor always downwind, but rather were oriented along the correct axis of migration, though in the wrong direction for the time of year. The reversal of direction was not associated with atypical temperature at the time of departure, a feature which might have explained why all migrants agreed in choosing the wrong flight direction.

A possible explanation of reversed move-

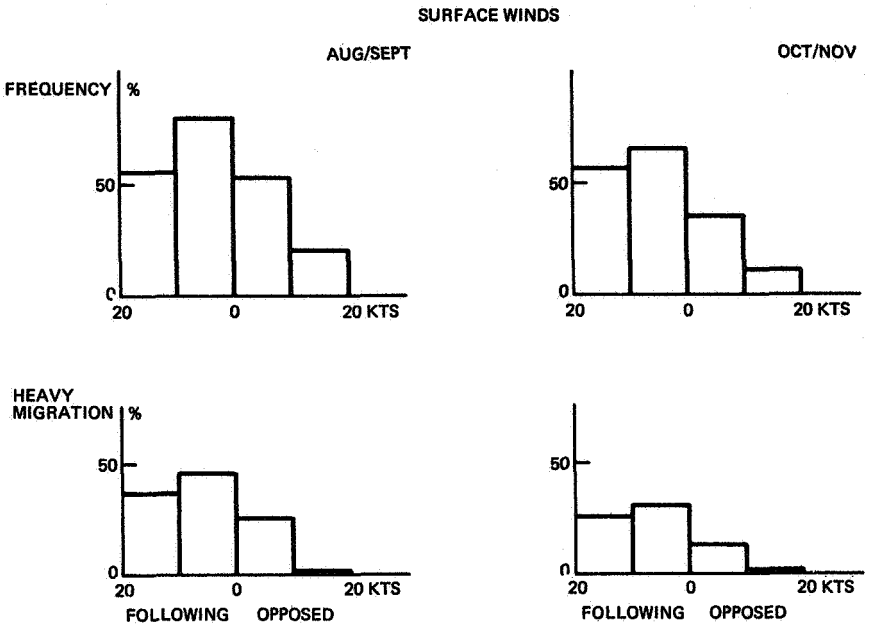

FIGURE 2. Relation between surface wind strength and direction and frequency and density of SSE migrations of passerines in northeast England, 1961 to 1963. Frequencies and densities are expressed as in Figure 1.

ments could be found if Rabøl's (ref. 20) hypothesis is established. Rabøl has suggested that the migratory route of a bird from its breeding grounds to its winter quarters can be thought of as the time-programmed movement of a "goal" area, so that on any chosen date during migration the migrant should be at a particular locality. If, for some reason, it had overshot this locality on a previous day's flight, then the bird might be expected to reverse its direction of flight to regain its correct (intermediate) goal, appropriate for that date. I am unhappy with this suggested explanation of reversed movements (even if Rabøl's hypothesis withstands test), as it seems most unlikely that a complete migratory flight (rather than few individuals) would overshoot the goal on a particular night, and thus be required to reverse their migration direction on the following night.

A further puzzle is that Emlen (ref. 21) believes that the choice of direction along the spring/autumn migratory axis is determined by the internal physiological state of the bird. By photoperiod manipulation he brought two groups of indigo buntings (*Passerina cyanea*) into the physiological states of spring and autumn migration, respectively, at the same time of year. When tested simultaneously under the spring planetarium sky, birds in spring condition oriented northward, those in autumnal condition southward. This experiment is, however, open to an alternative explanation: that the seasonal direction of migration is determined by the direction of the daily change in photoperiod. The birds Emlen brought into spring migratory condition experienced increasing photoperiods before their orientation was tested; those brought into autumn condition experienced

decreasing photoperiods. This suggests a hypothesis (as yet untested) for the occurrence of reversed migrations—that actual daylength on the date of the reversed flight was in some way different from those on previous days. More specifically, in autumn, I hypothesize that the daylength on the date of the reversed flight would be measured by the birds as being longer than on previous days (rather than shorter, as would be expected). This could result if a clear morning followed several days with cloudy mornings. Alternatively, since there is a circadian rhythm of photosensitivity (ref. 22), light intensities at particular times of day might be important.

Clearly the phenomenon of reversed migration requires further attention from radar ornithologists.

CHANGES IN FLIGHT DIRECTION DURING MIGRATION

Most of the small passerine night migrants which leave England in autumn are seen by radar to depart in directions east of south. Yet many species later reach Western Iberia, SSW of England, as shown by recoveries of banded birds. I have argued that the SSE departure direction allows migrants to fly partly with the wind on many nights when the same wind would be opposed to a direct SSW track (fig. 3). The migrants must change direction toward the west somewhere in southern France, allowing them to reach Portugal where they rest and eat. Although this may also require them to fly into the wind, the westerly winds in southern France are less strong than those in Britain. (The reason is that Britain is closer to the track of the low-pressure weather systems.) Hence the demands on a migrant are less (ref. 4). Also, movement into a headwind would take place overland instead of across the Bay of Biscay, so that a tired migrant could land safely, if necessary. In summary, the migration routes taken by many species seem to be a compromise between the need to reach a stopping area by the shortest way, and the need to avoid migration into strong headwinds if a preferred track is to be maintained.

In contrast to the large number of recoveries of banded passerine migrants in Iberia, very few recoveries of the same species have been made in the area where they are thought to change their direction of migration. Hence it seems probable that they do not need to land to change their course. This suggests that their map-sense is operative in flight. Further documentation is given by Evans (ref. 4).

It has been assumed in the foregoing discussions that birds fly along compass directions rather than along great circle routes. For chiefly north-south migrations, a migrant would save an insignificant distance by following a great circle route. However, for long east-west migrations, the great circle route would be preferable, e.g., at latitude 60° a 5000-km journey along the line of latitude could be shortened by more than 350 km by great circle course. However, to follow the latter course the migrant would need to change its compass heading continually, and this seems unnecessarily complicated unless it is performed incidentally, as a consequence of the method of navigation used.

CONCLUSIONS

The observations reviewed in this paper give more information on orientation processes than on navigation itself. For example, the migrants' ability to compensate for drift by the wind means that they are able to maintain an orientation in flight (but it tells us nothing of the way in which the orientation is first established). The unknown way in which drift is detected, and corrected for,

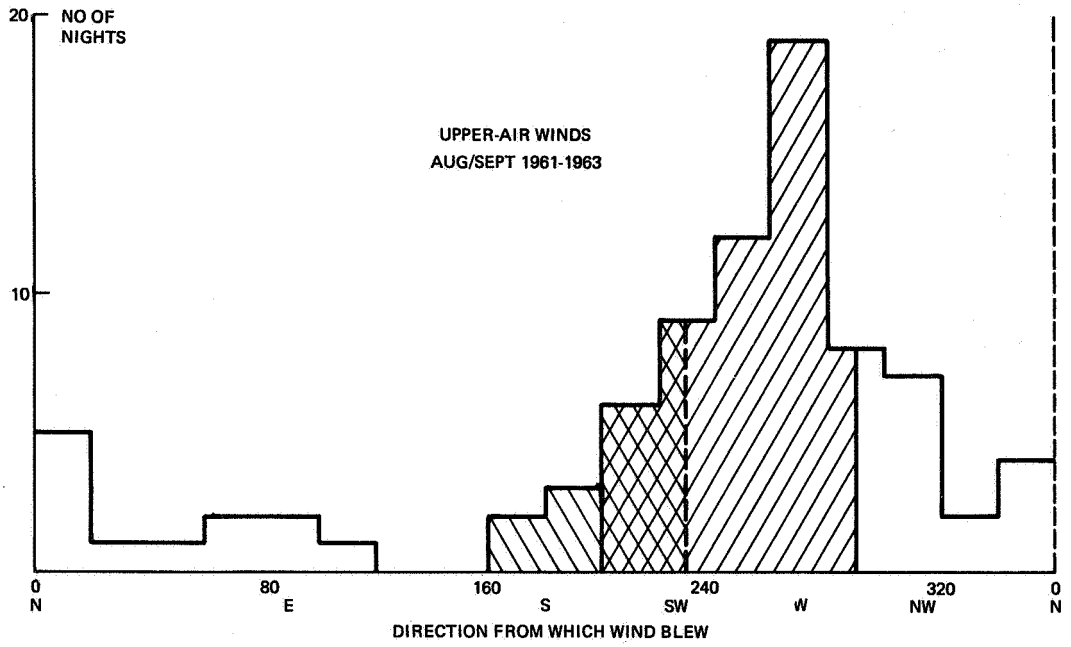

FIGURE 3. Distribution of upper-air (915 m) wind directions in August and September 1961 to 1963. Predominance of westerly winds is clearly shown. Winds from between SSW and WNW are opposed to a direct SSW flight from northern England to Iberia. By departing in a SSE direction, migrants convert a large proportion of these winds into partly following winds.

may or may not be related to the methods of long-distance navigation.

It seems clear that migrants are able to use more than celestial cues for orientation, as shown by the regular departures under total overcast and even through fog at ground level. Furthermore, the first journeys of certain long-distance migrants are more complex than the simple direction-and-distance movements demonstrated for starlings. Reorientation after displacement occurs; it is not known whether the new headings chosen by the migrants are indicative of their ability to navigate to an intermediate goal on the migratory route, or whether the new headings represent compromises between the standard direction of migration and the displacement directions. Insofar as navigation may take place by a map-and-compass process, it would seem to be used in flight, since changes in the direction of migration probably occur then. But radar studies have given no indication of the nature of the coordinate system used.

DISCUSSION

WILLIAMS: How did you identify the different groups of birds? You said some were waders (shorebirds) and some were passerines.

EVANS: Three methods were used to separate these groups—their times of departure, the departure localities, and their flight speeds. Waders departed between 1 and 2 hr before sunset from a limited number of coastal localities, well known as resting places for these species in northern Britain. Passerines departed from the whole land mass about 30 to 45 min after sunset. In August and September the mean flight speed of passerines was about 20 kt, whereas waders flew at over 30 kt; the

radar echoes from wader flocks were also much brighter than those from passerines. (Echo and flight speed differences between waders and passerines were much less in October and November and were not used to characterize the groups.) Details of species involved in the migrations are given in references 4, 5, and 16.

BRUDERER: Did you calculate the mean of individual headings on each night? Wouldn't the spread in individual headings be greater than in tracks on a single night?

EVANS: In my attempts to establish whether birds correct for wind drift, I worked with average track directions, assessed visually from the time-lapse films. From these I obtained an average heading for each night flight, by allowing appropriately for the wind velocity. I then compared night-to-night variation (spread) in average track directions with night-to-night variation in average headings. I am aware that Eastwood (ref. 23) has shown that on a single night, even if birds are drifted from preferred headings, the spread in resultant tracks can be less than in the headings. However, as I pointed out in my review of his book (ref. 24), Eastwood's analysis is irrelevant to the night-to-night comparisons made by several radar ornithologists, including myself.

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